Resumen

Los restos fósiles conservados en los sedimentos del Pleistoceno Medio de la cueva de Aldène (Francia) indican que al menos ocho especies diferentes ocuparon en algún momento la cueva. ***Myotis myotis***, es la especie más frecuente y ha sido identificada en todos los niveles con Quirópteros. La altísima proporción de dientes sin desgaste, e incluso algún elemento de la dentición decidua hallados en un par de niveles permite reconocer que la cueva se utilizó como refugio para las colonias de cría de esta especie. En cietos niveles los restos de ***Myotis myotis*** se encuentran asociados a los de otras especies de los géneros ***Myotis***, ***Rhinolophus***, ***Pipistrellus, Barbastella*** y ***Miniopterus***. Alguna de estas especies, aunque representadas por un menor número de restos, son indicativas de factores climáticos y paisajísticos, aportando datos adicionales a las interpretaciones paleoecológicas realizadas a partir de los roedores.

Palabras clave: Quirópteros, Rhinolophidae, Vespertilionidae, Miniopteridae, Pleistoceno medio, Francia.

Abstract

The fossils preserved in the sediments of the cave of Aldène show that this cave was used as a roosting place by at least eight different bat species during the Middle Pleistocene. Myotis myotis ***is the species best represented, and occurs at all the levels with bat remains. The high proportion of unworn teeth found of this species, together with some deciduous elements preserved at two different levels suggest the cave was occupied by nursery colonies.*** M. myotis ***occasionally shared the cave with other bat species from the genera*** Myotis, Rhinolophus, Pipistrellus, Barbastella ***and*** Miniopterus. ***Although these accompanying species are not so well represented in the associations, they provide interesting data concerning variations in the climatic conditions, to be compared to the interpretations carried out on the basis of the rodent fauna.***

Key words: Chiroptera, Rhinolophidae, Vespertilionidae, Miniopteridae, Middle Pleistocene, France.

The fossil Middle Pleistocene bats from the Cave of Aldène (Hérault, France)

Paloma Sevilla* & Jean Chaline**

Introduction

The bones and teeth of bats are rather frequent in Pleistocene cave deposits. They are often found together with other microvertebrates and occasionaly at the same levels that contain lithic industry. However, they are frequently overlooked to the point that our knowledge of this fauna during the Pleistocene can still be considered very incomplete. There are several reasons for this attitude. One of the reasons is that these fossils are usually set aside because of the higher interest of the paleontologists on the rodent fauna. Moreover, they are usually preserved as isolated teeth; the relatively similarity of the dental morphology makes the task of identifying the species apparently impossible. This has also led to the impression that the species have undergone no changes since the lower or middle Pleistocene, thus giving no information on the chronology of the deposits. However, these reasons are only partially justified: several papers have been published with detailed descriptions of the dentition of different species, thus permitting to recognise them from isolated teeth (Menú, 1985; Sevilla, 1986; Menú y Popelard, 1987); available data show that bats have undergone changes not only in size but also in certain dental characters during the Pleistocene, and finally, that changes in climate and landscape have determined variations in the geographic distribution of some species. Thus, further research on the fossils of bats preserved in Pleistocene localities is neccessary; it will no doubt contribute to a better understanding of recent patterns of distribution and might as well give a clue so as to the factors that may be leading to recent changes in the relative abundance of some species.

* Departamento de Paleontología. Facultad de Ciencias Geológicas e Instituto de Geología Económica, CSIC. Universidad Complutense. E-28040 Madrid.

** UMR CNRS Biogéosciences. Centre des Sciences de la Terre. Université de Bourgogne. 6, Bd. Gabriel. 21100 Dijon. Francia.

The locality

The cave of Aldène is situated close to the town of Cesseras on the right bank of the river Cesse, an afluent of the Aude (Fig. 1). It consists of a complex series of galleries developed in Lower Eocene limestones, filled with sediments rich in phosphates, a great part of which were extracted between 1888 and 1937, leaving little behind. The cave was known for its paintings on the walls, as well as lithic industry. The damage on the few remaining sediments caused by visitors to the cave looking for stone implements and bear bones made necessary on years 1971 and 1972 the excavation of what was left. These excavations, led by Drs. Barral and Simone, were carried out mainly at the entrance of the cave and at certain spots in some galleries. This paper refers to the fossil bats found in the main outlier preserved on the northern wall of the hall at the entrance of the cave, referred to as T1 by Barral and Simone (1974). A detailed description of the sedimentology of the deposits is given in Baïssas (1974).

Barral and Simone (1974) recognised seventeen different levels at T1, named from the surface to the base, A to M (Fig. 2). These levels were grouped into three major units: a lower unit, consisting of levels M to I, an intermediate unit, comprising levels H to F and separated from the lower unit by a stalagmitic

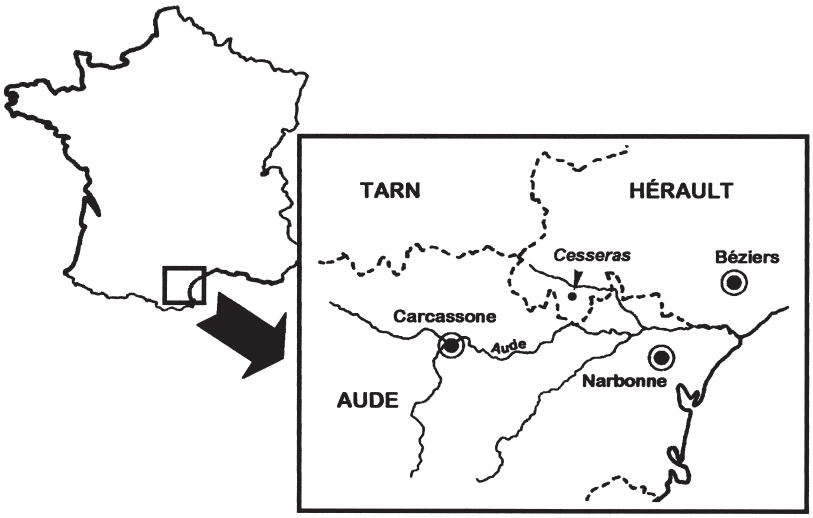

Fig. 1. Geographic situation of the Cave of Aldène.

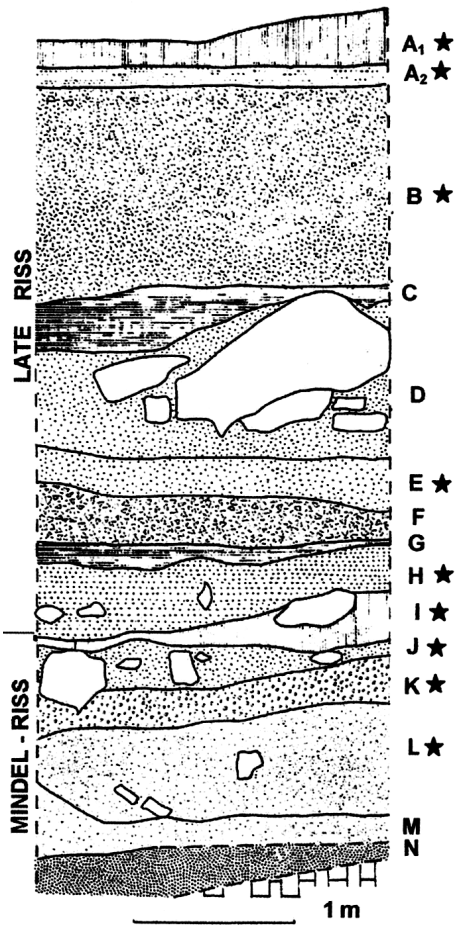

Fig. 2. Schematic profile of the sediments of the cave of Aldène. The levels with fossil bats are indicated by (*).

layer, and finally a third unit with levels E to A. Lithic industry was not specially abundant at T1, the majority of the implements were located in levels K, H and G. The fossils of big mammals were also scarce, except at level I, the associations varying from one unit to the other. Fossils of bear (*Ursus deningeri* or *U. spelaeus*) and deer (*Cervus elaphus*) were found in the three units; in the lower unit they were associated to other herbivores (*Equus caballus*, *Dicerorhinus mercki, Hemitragus jemlahicus*) and a carnivore (*Hyaena prisca*); in the intermediate unit to large bovids, and in the upper unit to *Equus caballus* and *Felis spelaea*. Regarding the age of the deposits at T1, the lower levels up to level I were dated as of Mindel-Riss age; the remaining levels up to A_1 as late Riss (Barral y Simone, 1974).

Small mammal bones were found at practically all the levels of T1; however they were not especially abundant except at level B. Nevertheless, the different associations enabled Chaline (1974) to recognise six distinct phases. The rodents of the first (levels M to J) and second phases (level I) indicated a lanscape of steppe and patchy woodland, characterised by a strong continental climate. Phases 3 (levels H to D_2) and 5 (levels C and B) were interpreted as of extremely continental climate with long winters, a slight improvement inbetween at phase 4 (level D_1). Finally, the rodents preserved at levels A_2 and A_1 (phase 6) indicate a temperate climate and a landscape covered with atlantic forest.

Simone *et alii* (2002) have recently published a paper which presents an update of the results on the researches led on the Middle Pleistocene deposits of Aldène, together with new data that lead to a reassesment of the previous interpretations. The levels of outlier T1 are grouped into two major units: the “upper layers” (H to A) and a “lower whole” (M to I); datings based on U/Th and ESR place level A_1 at climatic stage 5.5 of Imbrie *et alii* (1984); the “lower whole” represents parts of climatic stages 13 to 11. Simone *et alii* (*op. cit.*) report as well the presence of *Maccaca sylvanus* and *Pliomys episcopalis* at level I.

Description of the material

Fossils of eight species of bats were found in ten levels of section T1 (Table 1). A total of 170 remains of these small mammals were identified. For the most part, the material consists of isolated teeth, except for several fragments of mandibles and maxillae, some of them carrying teeth. In spite of the fragmentation, the teeth are relatively well preserved and

TABLE 1. Number of remains representing each species at the levels of Aldène with fossil Chiroptera.

	R. ferrumequinum	*R. mehelyi*	*M. myotis*	*M. daubentoni*	*M. bechsteini*	*P. pipistrellus*	*B. barbastellus*	*M. schreibersi*
A_1			14					
A_2	1		41					
B_1			12					
E			1					
H			3					
I	2	2	10	2	1	2		13
J_2			3	1		1		
K_1			1					1
K_2			17				1	1
L			35					5

only in five specimens corrosion was observed. As is frequent with this type of material, the damage in the teeth consists mainly on missing roots or styles. Even though level L was reported by Barral and Simone (1974) as being rich in bones of Microchiroptera, level A_2 has produced a similar number of remains.

The fossils were identified following the criteria described in Sevilla (1986), and Menú & Popelard (1987) and compared with recent specimens loaned from the Museo de Ciencias Naturales of Madrid. Measurements were taken following Storch (1974) and Sevilla (1988). Ecologic requirements and recent distributions of the species were taken from Mitchell - Jones *et alii* (1999).The material on Figures 3 to 6 was drawn with camera lucida on a Wild M-8 microscope, and the pictures of Figure 5 were taken with a camera Leica DC-300 fixed to the microscope.

Family RHINOLOPHIDAE GRAY, 1866
Genus ***Rhinolophus*** LACÉPÈDE, 1779
Rhinolophus ferrumequinum (SCHREBER, 1774)
(Fig. 3, *1* - *3*)
Material
Level A_2: 1 fragment of right maxilla carrying M^2M^3
Level I: 1 left upper canine; 1 left M^3
Measurements
M^2: 2,12 x 2,58
M^3: 1,50 x 2,25; 1,64 x 2,35
Remarks: *Rhinolophus ferrumequinum* is represented in Aldène by only three remains. The upper canine, found at level I, is very damaged and practically the whole root is missing. On the lingual face, the crown presents a rounded longitudinal rib that extends from the cingulum to the apex of the tooth. A similar rib has been described in *Rhinolophus* cf. *ferrumequinum* from the Lower Pleistocene of Hungary (Topál, 1963) and is also observed in some recent specimens of the species, though flat surfaces are more common. The tooth is moderately worn on its distal ridge. The development of the talon of the M^2 from level A_2 agrees with that of recent specimens, and is reduced as compared to the larger talons observed in *R. macrorhinus* and *R. postdelphinensis* , possible Pliocene and lower Pleistocene ancestors of *R. ferrumequinum* (Topál, 1979). As is observed in the recent species, the two M^3 of *R. ferrumequinum* of Aldène lack a postmetacrista and the premetacrista is reduced to a half the length of the postparacrista.

R. ferrumequinum is not uncommon in Pleistocene cave and karst localilties, although it is rarely represented by a high number of specimens. Even though the first records of this species in Europe date from the Lower Pleistocene, its fossils in France up to now were only known from Upper Pleistocene localities such as Fontechevade (Schreuder, 1959) or L'Hortus (Jullien, 1972).

Recent *R. ferrumequinum* is distributed through southern and central Europe; it is a cave-dwelling species and is known to require warm temperatures in its roosting places, especially during the spring. Its occurence at levels I and A_2 are indicative therefore of a warm climate for those levels.

Rhinolophus mehelyi MATSCHIE, 1901
(Fig. 3, *4* and *5*)
Material
Level I: 1 right M^1; 2 right M^2
Measurements
M^1: 1,87 x 2,00
M^2: ? x 2,00
Remarks: this species is poorly represented in Aldène: only three upper molars were found at level I, the three of which are slightly worn. They present very short talons and a straight distal margin, that together with the size, fit with recent *R. mehelyi*. Though fossils of this species are known since the lower Pleistocene, it is quite less frequent than *R. euryale*; this is probably due to its strong mediterranean character, that can also be inferred for the Pleistocene since fossils of *R. mehelyi* have been described in several southern european localities such as Ghar Dalam in Malta (Storch, 1974) or Cueva Victoria in southern Spain (Sevilla, 1988). The occurence of *R. mehelyi* at level I again supports the interpretation of a warm climate for this level. Fossils of *R. mehelyi* in France have been described in the Upper Pleistocene and Holocene levels of L'Hortus (Jullien, 1972), but were not known in the Middle Pleistocene.

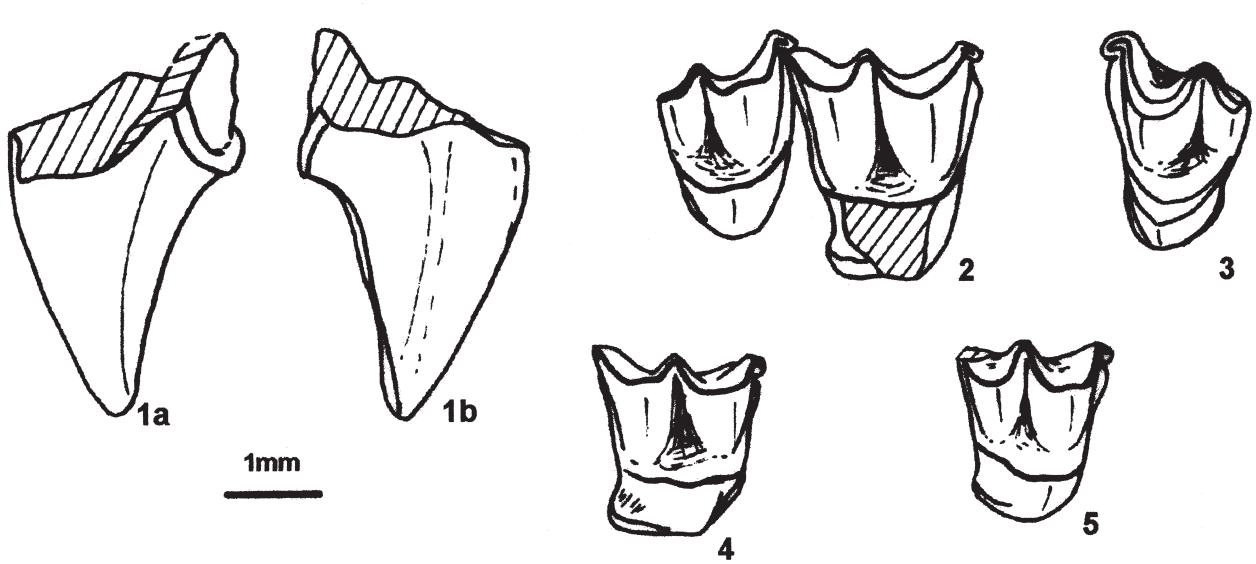

Fig. 3. *Rhinolophus ferrumequinum.* 1: left upper canine (a: labial; b:lingual); 2: right M^2M^3; 3: left M^3. *Rhinolophus euryale*. 4: right M^1. 5: right M^2.

Recent *R. mehelyi* is distributed in southernmost Europe in environments of warm and open landscapes. It exclusively roosts in caves; during hibernation it forms small groups, sometimes mixed with other species.

Family VESPERTILIONIDAE GRAY, 1821
Genus ***Myotis*** KAUP, 1829
Myotis myotis (BORKHAUSEN, 1797)
(Fig. 4, *1 - 12*; *17*)
Material:

Level A_1: 1left I^2; 1right P^2; 2 leftP^3; 1 right P^4; 1right M^1; 1 left M^3;1 left lower canine; 1 right P_2; 2 left P_2; 1 left P_3; 1 right M_1; 1 left M_3

Level A_2: 2 right I^1; 1 left I^1; 1 right I^2; 1 right upper canine; 1 left upper canine; 1 right P^2; 2 right P^4; 1 left P^4; 2 right M^1; 1 right M^2; 1 left M^2; 1 right M^3; 2 left M^3; 1left I_3; 2 left lower canines;1 right P_2; 1 left P_2; 2 right P_3; 2 left P_3; 3 right P_4; 2 left P_4; 3 right M_1; 3 left M_1; 1 right M_2; 1 left M_2; 1 right M_3; 1 fragment of left mandible with deciduous teeth and permanent lower canine, P_2, P_4 and M_1 erupting.

Level B_1: 1 left M^1; 1 right M^3; 1 right I_1; 1 left lower canine; 1 left P_2; 1 right P_2; 1 left P_3; 1 right P_4; 1 right M_1; 1 left M_2; 1 right M_3

Level E: 1 left P_4

Level H: 1 right P^3; 1 right M^1; 1 left M_1

Level I: 2 left I^1; 1 right I^2; 1 right upper canine; 1 right P^2; 1 right M^1; 1 right M^3; 2 right M_1; 1 left M_1

Level J_2: 1 right M_2; 1 left I_3; 1 right lower canine

Level K_1: 1 right P_4

Level K_2: 2 left I^1; 1 left I^2; 1 left upper canine;2 left M^1; 1 right M^1;1 left M^2; 1 left M^3;1 right I_1; 1 right lower canine; 1 left P_3; 1 left P_4; 1 right M_1; 2 right M_2;1 deciduous tooth

Level L: 2 left I^1; 2 left I^2; 1 left P^2; 1 right P^4; 1 left P^4; 1 right M^1; 3 left M^1; 1 right M^3; 1 left M^3; 1 left I_1; 1 right I_3; 1 left I_3; 1 right lower canine; 1 left lower canine; 1 right P_2; 2 left P_3; 3 left P_4; 1 right M_1; 2 left M_1; 2 left M_2; 1 fragment of left mandible with M_2M_3; 2 fragments of left mandibles with M_3

Measurements: (see Table 2).

Remarks: *Myotis myotis* is by far the best represented bat in Aldène. There are fossils of this species at ten levels; at four of them it is the single species that occurs. Remains of every tooth, including incisors, small premolars and even one isolated deciduous tooth have been preserved. The morphology agrees with that of recent *M. myotis*; however, the range of variation in size is wider than what is observed in recent *M. myotis*, to the point that some specimens fall within the sizes of recent *M. blythi*. However, no specimen presents the morphologies that characterise *M. blythi*. Thus, the development of the preparacrista in the M^3 is similar to that of recent *M. myotis,* the values of the degree of reduction of the talonid in the M_3 index (Mein, 1975) range from 41,1-44,3 and are normal values for *M. myotis*; and in the only unbroken mandible preserved, the height of the mandibular ramus is 6,14 mm, also a typical *M. myotis* value.

A great part of the teeth are unworn, some clearly belonging to very young specimens; at level K_2 an isolated deciduous tooth was found, and at level A_2, a mandible with permanent teeth erupting and two hooked deciduous teeth at the positions of P_3 and M_1 (Fig. 5). The preservation of deciduous teeth of bats in fossil localities is rare, since they are replaced soon after birth and poorly calcified; however, they have been described in

TABLE 2. Measurements (in mm) of the fossil ***Myotis myotis*** of the cave of Aldène.

	n		
I_1	1	L	0,77
		W	0,32
I_3	2	L	0,80 - 0,96
		W	0,74 - 0,80
lower C	8	L	1,12 - 1,35
		W	1,29 - 1,35
P_2	4	L	1,00 - 1,03
		W	1,03 - 1,12
P_3	9	L	0,67 - 0,96
		W	0,96 - 1,12
P_4	11	L	1,25 - 1,45
		W	0,96 - 1,19
M_1	15	L	2,00 - 2,45
		W_1	1,16 - 1,67
		W_2	1,45 - 1,75
M_2	7	L	2,12 - 2,58
		W_1	1,12 - 1,61
		W_2	1,45 - 1,70
M_3	3	L	1,80 - 2,09
		W_1	1,29 - 1,41
		W_2	0,74 -0,93

	n		
I^1	4	L	0,80 - 0,83
		W	0,51 - 0,64
I^2	3	L	0,67 - 0,90
		W	0,64 - 0,83
upper C	4	L	1,58 - 1,87
		W	1,29 - 1,48
P^2	6	L	0,80 - 0,96
		W	0,96 - 1,09
P^4	4	L	1,70 - 2,00
		W	1,29 - 1,58
M^1	13	L	2,29 - 2,80
		W	2,25 - 3,06
M^2	2	L	2,32 - 2,74
		W	2,90 - 3,22
M^3	8	L	1,77 - 1,93
		W	2,58 - 2,80

the Upper Pleistocene locality of La Carihuela in Spain (Sevilla, 1988) and at the Eocene locality of Messel (Sigé *et alii*, 1998). At levels A_2, I and L, unworn teeth were found together with a few very worn teeth.

M. myotis is frequently found in Pleistocene fossil localities, usually represented by a high number of specimens. Variations in the range of size of this species seem to have taken place during the Pleistocene, with larger specimens in the Lower Pleistocene and slightly smaller sizes in some Middle Pleistocene localities (Sevilla, 1988). It is possible that fossils from the Middle Pleistocene described as *M. blythi* are in fact small *M. myotis.*

M. myotis has been cited in Upper Pleistocene localities of France such as Fontéchevade (Schreuder, 1959) and L'Hortus (Jullien, 1972); fossils of *Myotis* cf. *myotis*, characterised by a slightly smaller size than the recent species, occur at the Middle Pleistocene of La Fage (Mein, 1965).

Recent *M. myotis* is widely distributed in Europe; it is a tolerant species, found in a wide variety of habitats. It is relatively tolerant to human presence and large nursing colonies are frequently found in the attics of buildings. It sometimes uses caves or mines as roosting sites the year round.

Myotis daubentoni (KUHL, 1819)
(Fig.4, *13 - 15*)
Material
Level I: 1 right P^4; 1 left M^2
Level J_2: 1 right upper canine
Measurements: upper canine: 0,93 x 0,70
P^4: 1,03 x 0,90

Remarks: Remains of this small species have been found at two levels of Aldène. The single canine of level J_2 is very chacteristic, with its semicircular cross section, flat inner surface and shallow furrow on the labial surface. The P^4 presents an anterolingual cusplet of intermediate development; the M^2 is damaged, the paracone completely missing, but several other important characters are observed, such as the rounded inner margin, and the postprotocrista, with a small but clear metaloph, labially directed. These characters agree with the morphology of recent *M. daubentoni*. *M. brandti,* close in size and morphology to *M. daubentoni*, presents, however, a lingual cusplet in the canine; the lingual cusplet of the P^4 is better developed and the M^2 is wider on the lingual margin and has a straight distal outline.

M. daubentoni is extremely rare as a fossil; up to now, it was only known from the Upper Pleistocene locality of Santenay (Sevilla, 1990). *Myotis delicatus* from Upper Pliocene and Lower Pleistocene localities of eastern Europe (Heller, 1936; Topál, 1963), a possible ancestor of both *M. daubentoni* and *M. brandti*, presents intermediate characters between these two species and a slightly larger size. In *M. delicatus*, the morphology of the upper canine and the M^2 is similar to that of recent *M. daubentoni*, whereas the anterolingual cusp on P^4 is larger and more similar to that of *M. brandti*.

M. daubentoni is nowadays one of the most abundant species in central Europe; however, it is relatively rare in southern Europe, since it is mainly found in environments of deciduous and mixed forests, close to lakes and ponds. During summer it uses hollow trees as shelters and hibernates in caves, where it can group forming large colonies.

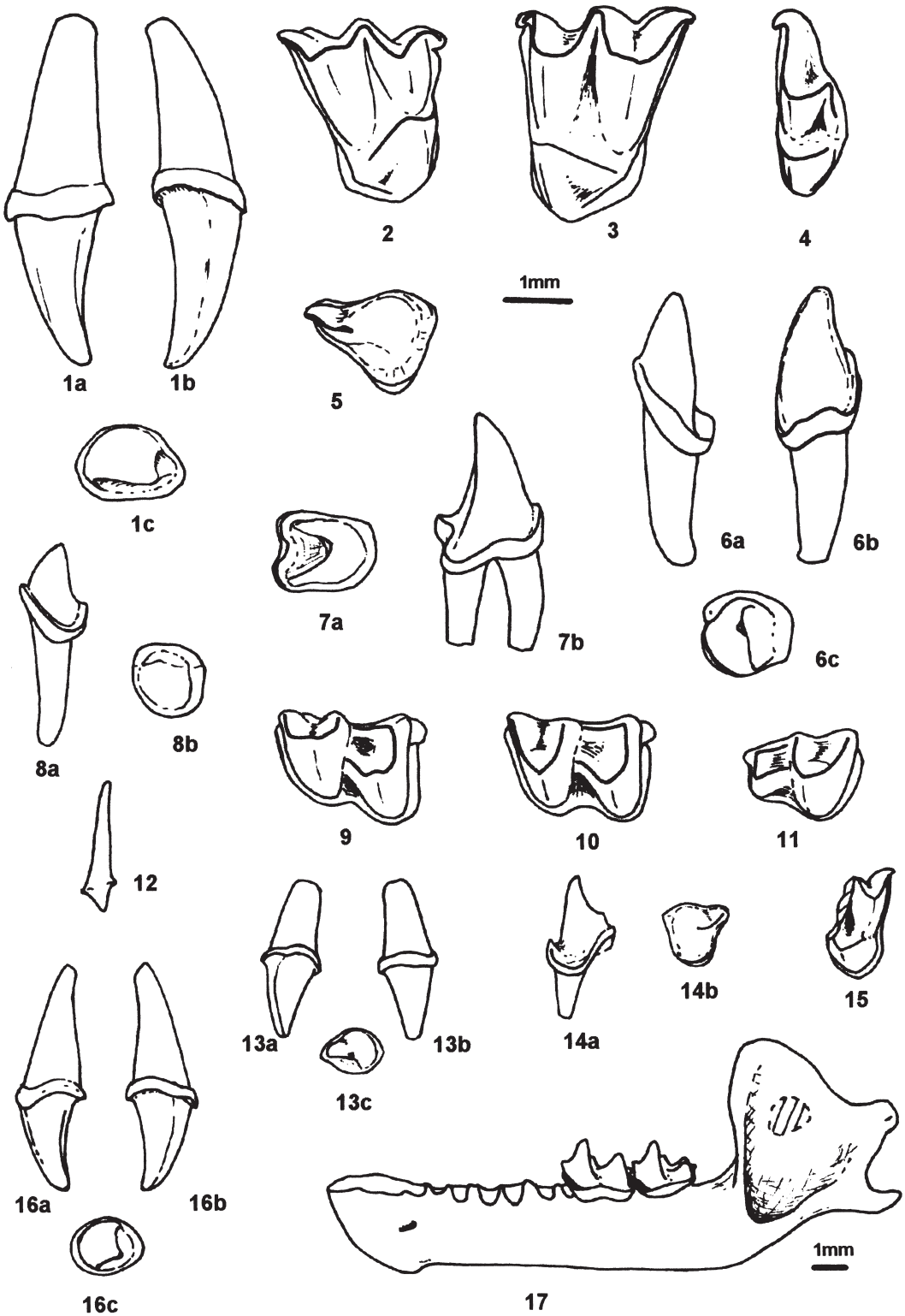

Fig. 4. *Myotis myotis.* 1: left upper canine (a:labial; b:lingual; c:occlusal); 2: right M^1; 3: left M^2; 4: left M^3; 5: right P^4; 6: left lower canine (a:labial; b:distal; c:occlusal); 7: right P_4 (a:occlusal; b:labial); 8: left P_2 (a:labial; b:occlusal); 9: left M_1; 10: left M_2; 11: right M_3; 12: upper deciduous tooth; 17: left mandible carrying M_2M_3
Myotis daubentoni . 13: right upper canine (a:lingual; b:labial; c:occlusal); 14: left P^4 (a: lingual; b: occlusal); 15: left M^2.
Myotis bechsteini. 16: left upper canine (a: labial; b:lingual; c:occlusal)

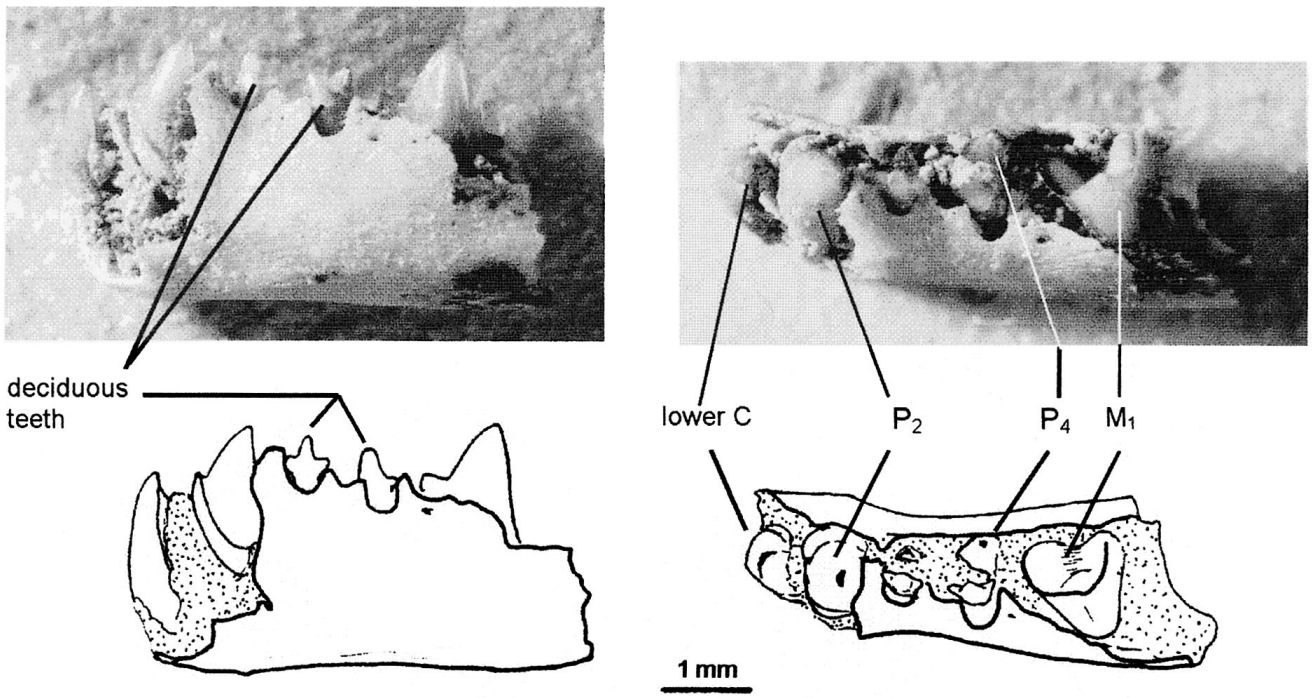

Fig. 5.*Myotis myotis*. Fragment of left lower mandible carrying two deciduous teeth and erupting permanent teeth (lower canine, P_2, P_4 and M_1)

Myotis bechsteini (KUHL, 1818)
(Fig. 4, *16*)
Material: Level I: 1 left upper canine
Measurements: upper canine: 1,06 x 0,90
Remarks: A single, slightly worn canine of *Myotis bechsteini* was found in Aldène. Its size and shape agree with the morphology observed in recent *M. bechsteini*. This species is very frequent in Pleistocene localities all over Europe, where a slightly larger size has been reported, giving place to the description of the subspecies *M. bechsteini robustus* Topál (1963). In France, *M. bechsteini* has been described in La Fage (Mein, 1975), where the remains indicate a slightly larger size than that of the recent species, but not so large as *M. bechsteini robustus*, and also in the Upper Pleistocene of Santenay (Sevilla, 1990); in both localities it is the most abundant species.

M. bechsteini is distributed in Europe in areas of mature deciduous forests and rarely hibernates in caves, in this case in groups of very low numbers. Considering it is one of the most common species in the fossil localities, and frequently represented by high numbers of remains, *M. bechsteini* must have been very abundant in Europe during the Pleistocene. An important decrease in its populations since historic times seems to be a consequence of recent deforestation processes.

Genus ***Barbastella*** GRAY, 1821
Barbastella barbastellus (SCHREBER, 1774)
(Fig. 6, *1*)
Material: Level K_2: 1 right upper canine
Measurements: upper canine: 1,00 x 0,80
Remarks: This single remain presents the characteristic morphology of the upper canines of the genus *Barbastella* with its elongate section and flat inner surface divided by a strong rib. The size agrees with that of recent *B. barbastellus*. The Middle Pleistocene species *Barbastella rostrata* (Topál, 1970) is slightly larger, with proportionately longer and narrower upper canines. *Barbastella barbastellus* occurs at several Pleistocene localities of Europe. Its known from the Lower Pleistocene of Hundsheim (Rabeder, 1972), where it is represented by the subspecies *B. barbastellus carnuti*, slightly larger than recent *B. barabastellus*. Its fossils in France are known in the Upper Pleistocene localities of Fontéchevade (Schreuder, 1959), L'Hortus (Jullien, 1979) and Santenay (Sevilla, 1990).

B. barbastellus is most common in central Europe and rare in southern Europe. It clearly prefers cooler climates and is most frequently found in upland and forest habitats. It roosts in hollow trees, and chooses cold places for its short period of hibernation, usually rock crevices or the entrance of caves, where it is found solitary or at most in small groups. For this reason it has been used as an indicator of colder climates during the Pleistocene.

Genus ***Pipistrellus*** KAUP, 1829
Pipistrellus pipistrellus (SCHREBER, 1774)
(Fig. 6, *2,3*)
Material
Level I: 1 M_3; 1 fragment of right mandible
Level J_2: 1 left M_2
Measurements
M_2: 1,12 x 0,64 x 0,70
M_3: 1,03 x 0,58 x 0,48
Remarks: only three remains of this small vespertilionid have been recognised at two levels of the lower unit of T1. Two lower molars, easy to recognise for their small size, nyctalodont pattern and narrow trigonid and a mandible, slender, with the ventrally projecting symphisis, present no differences with the recent species in the size or in the morphology.

In spite of the ubiquituous nature shown by recent *P. pipistrellus*, it is rarely present in fossil associations. It occurs, however, since the lower Pleistocene in Ghar Dalam, Malta (Storch, 1974), where fossils with no differences with the recent species have been described, and it seems to have remained unchanged since then. In the few Pleistocene localities where it has been described, it is always represented by very few remains. In France, it is known from the Upper Pleistocene layers of L'Hortus (Jullien, 1972).

This species is widely distributed in Europe. It occasionally is found hibernating in caves, but it is more frequently found in buildings, usually grouped forming large colonies. It hibernates for a short period, and is quite tolerant to cold conditions. Its present day abundance and low frequency in Pleistocene localities may indicate an increase in the numbers of this species during historic times, probably favoured by its capacity to use human constructions as shelters.

Family MINIOPTERIDAE MEIN & TUPINIER, 1977
Genus ***Miniopterus*** BONAPARTE, 1837
Miniopterus schreibersi (KUHL, 1819)
(Fig. 6, *4 - 10*)
Material
Level I: 1left I^1; 3 right upper canines; 5 left upper canines;1 left M^2; 1 left P_2; 1 left M_2; 1 right M_3
Level K_1: 1 left upper canine
Level K_2 : 1 right P^4
Level L: 1 right upper canine; 1 right P_2; 1 right P_3; 1 left M_1; 1 left M_3
Measurements
I^1: 0,58 x 0,38
upper canines (n = 7): 1,03 - 1,12 x 0,80 - 0,87
M^2: 1,48 x 1,93
Remarks: *M. schreibersi* is the second best represented species in Adène; it outnumbers *M. myotis* at level I. Its teeth are very characteristic, with long and slender cusps and agree both with the morphology and the size observed in the recent specimens of the species. The most frequent element in the sediments of Aldène are the upper canines, with a rounded cross section, and two longitudinal grooves both on the labial and on the lingual surfaces. A single P^4 is preserved at level K_2, and though strongly damaged, the large and wide talon characteristic of this species is easily recognised. An upper canine, an M^2 with its rectangular outline, and several lower nyctalodont molars, with sharp and narrow cusps, have also been identified as of *M. schreibersi*.

All the specimens at level I seem to belong to juvenile individuals since no wear is observed.

Fossils of *M. schreibersi* are known since the Upper Pliocene without changes in size or morphology. It has been described in the french Upper Pleistocene locality of L'Hortus (Jullien, 1972). Even though it is known to form large colonies, sometimes of several thousands of individuals, it is usually represented by low numbers at the fossil localities. Its recent distribution extends throughout southern Europe, and because of its preference for warm roosting places, with temperatures round 10º C, it has been used in fossil sites as indicator of relatively warm climate.

General remarks

With its 170 fossils of bats, the cave of Aldène cannot be considered as a rich locality for this fauna, especially if compared with some Pleistocene cave deposits where bats are represented by thousands of remains. Nevertheless, the material preserved does not lack interest. On one hand, several species are reported for the first time in the Middle Pleistocene of France (*R. ferrumequinum*, *R. mehelyi*, *B. barbastellus* and *M. schreibersi*), two of which are rare in cave deposits (*P. pipistrellus* and *M. daubentoni*); on the other, the ocurrence of some good paleoclimatic indicators (*M. schreibersi*, *R. ferrumequinum*, *R. mehelyi*) permit to carry out palaeoenvironmental interpretations based on this fauna.

If the origin of the phosphates of level M was the guano of bats (Simone *et alii*, 2002), the cave must have sheltered large colonies of thousands of individuals, and the conditions in the surroundings of the cave, or in the cave itself, must have been optimal. No information is left about which species might have formed these large colonies; the guano must have destroyed any organic matter under the colony, giving no chance to bones or teeth to have been preserved. The environmental conditions seem to have changed afterwards, since the number of remains found in the onlying levels is relatively low, especially in the levels grouped as the upper unit.

Considering the two main units of Simone *et alii* (2002), an important difference is observed in the diversity and composition of the bat associations. In the lower unit (levels L to I) a relatively wide variety of species has been preserved, whereas in the upper unit (levels H to A_1)a very low diversity is observed.

Myotis myotis is the species that more frequently dwelt the cave: it is only is missing at the levels where no fossil bats have

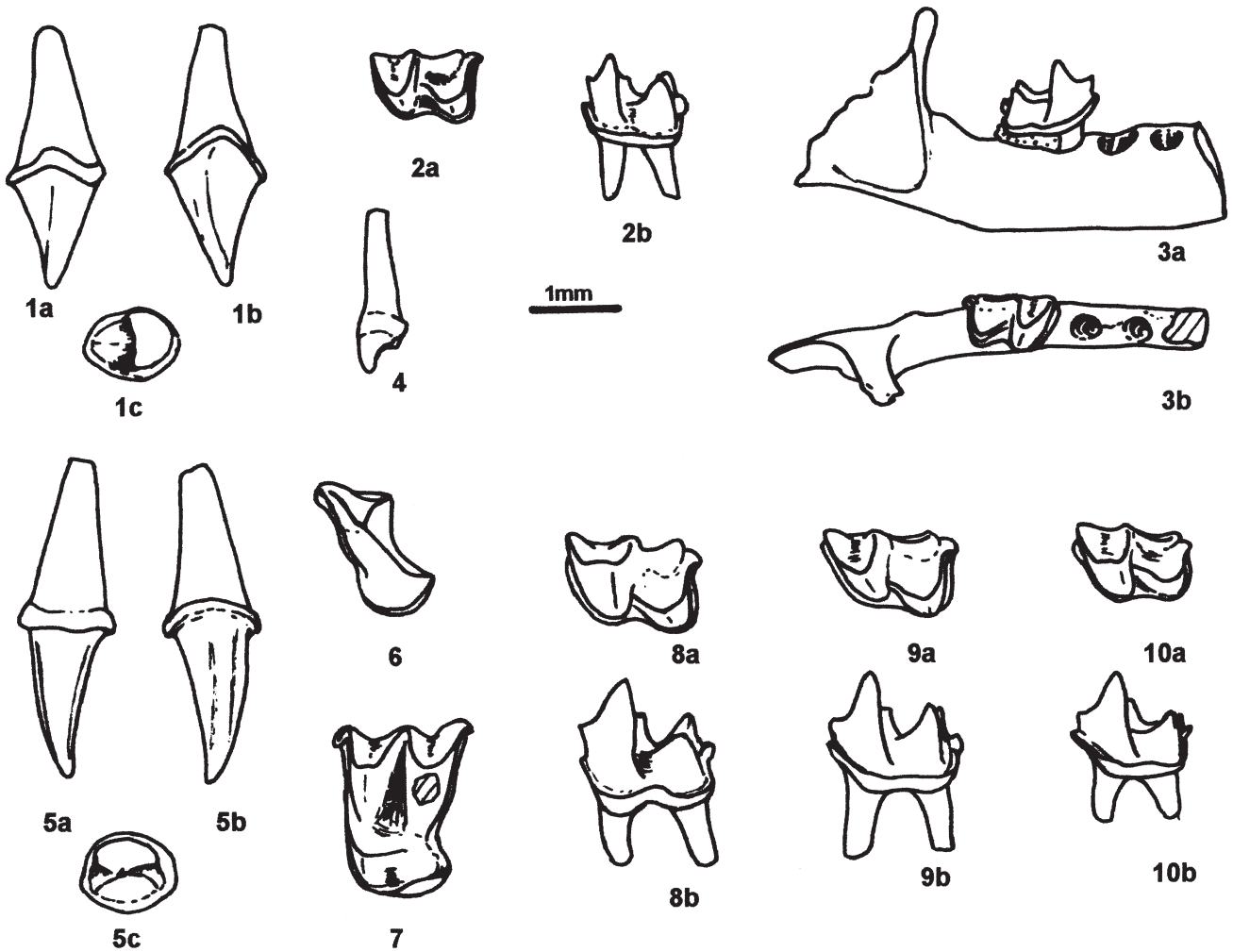

Fig. 6. *Barbastella barbastellus*. 1: right upper canine (a:labial; b:lingual; c:occlusal).
Pipistrellus pipistrellus. 2: left M_2 (a:occlusal; b:labial); 3: fragment of right mandible with M_3 (a:labial; b:occlusal)
Miniopterus schreibersi. 4: left I^1; 5: left upper canine (a:labial; b:lingual; c:occlusal); 6: fragment of right P^4; 7: left M^2; 8: left M_1 (a:occlusal; b:labial); 9: left M_2 (a:occlusal; b:labial); 10: left M_3 (a:occlusal; b:labial).

been found. Considering the patterns of mortality in bats, which is higher either in early stages of life or during hibernation among aged indivuals (Hill and Smith, 1984), the high proportion of unworn teeth and the deciduous teeth from two different levels indicate *M. myotis* used the cave of Aldène mainly as a nursery roost; and occasionally, as a winter shelter. *M. myotis* appears associated to *M. schreibersi* , the second best represented species, in all the lower unit except at level J_2. In this level instead, *Myotis daubentoni* and *Pipistrellus pipistrellus* were found. The last level of the lower unit, level I, presents the highest diversity, with seven different species represented. In the upper unit, *M. myotis* is the only species that occurs, except at level A_2 where it is found with *R. ferrumequinum*.

The bats preserved in the different levels at T1 indicate the following evolution in the lanscape and climate during the Mindel-Riss and Late Riss at the area of Aldène:

- a landscape of forests and relatively warm climate is interpreted for the whole of the lower unit (levels M to I) where *M. schreibersi* occurs, with a more continental character at levels K_2 and J_2, as inferred by the presence of *B. barbastellus*, *M. daubentoni* and *P. pipistrellus*. The high diversity observed at level I, where 7 species occur together, indicate an important development of forests and a temperate humid climate. This agrees with the recent discovery of a well preserved mandible of *Maccaca sylvanus* at this level (Simone *et alii*, 2002).
- the decrease in the diversity observed in the upper unit (levels H to A_1), where only *M. myotis* occurs, except at one level, is probably due to a reduction of the forests and an important change towards a colder climate, with a shorter summer season. A slight improvement towards warmer temperatures may be inferred for level A_2, where *R.*

ferrumequinum occurs. This interpretation agrees with that based on the rodents and the palinology, which indicate boreal climate with the development of steppe vegetation and a reduction of forest cover.

As a final comment, we can say that the cave of Aldène may serve as an example of how the study of fossil bats preserved at Pleistocene cave deposits, in spite of fragmentation, may prove an interesting source of information and therefore, should not be left unstudied.

Acknowledgements

The authors wish to thank the French MRC and the Spanish MEC for financing a ten month stay in 1987 of the first author at the Centre des Sciences de la Terre of the Université de Bourgogne, during which the material described in this paper was studied and had remained until now unpublished. The fossils described in this paper were compared with recent specimens of the species Myotis nattereri, M. daubentoni, Rhinolophus ferrumequinum, R. euryale that were loaned from the Museo de Ciencias Naturales de Madrid.

Bibliography

Baïssas, P. (1974): "Étude sédimentologique sommaire du remplissage de la grotte d'Aldène (Cesseras, Hérault)". *Bulletin du Musée d'Anthroplogie préhistorique de Monaco*, 18: 69-88.

Barral, L. y Simone, S. (1974): "Le Mindel-Riss et le Riss à la grotte d'Aldène (Cesseras, Hérault)". *Bulletin du Musée d'Anthroplogie préhistorique de Monaco*, 18: 69-88.

Chaline, J. (1974): "Les Rongeurs de la Grotte D'Aldène. Une nouvelle séquence climatique du Pléistocène moyen". *Bulletin du Musée d'Anthroplogie préhistorique de Monaco*, 19: 5-20.

Heller, F. (1936): "Eine Oberpliozäne Wibertierfauna aus Rheinhessen". *Neues Jahrbuch für Mineralogie und Paläntologie, Abteilung B*, 76: 99-160.

Hill, J.E. & Smith, J.D. (1984): *Bats. A Natural History.* British Museum (Natural History). Londres. 243 págs.

Imbrie, J.; Hays, J.D.; Martinson, D.G.; McIntyre, A.; Mix, A.C.; Morley, J.J.; Pisias, N.G., Prell, W.L. & Shackleton, N.J. (1984): "The orbital theory of Pleistocene climate: support from a revised chronology of the marine ?^{18}O record". In A. Berger, J. Imbrie, J. Hays, G. Kukla, G. & B. Satzman (Eds.): *Milankovitch and climate. Part I*: 269-305.D. Reidl Publishing Co.

Jullien, R. (1972): "Les Chiroptères du Würmien II de la Grotte de l'Hortus (Valflaunès, Hérault)". *Études Quaternaires*, 1: 247-265.

Mein, P. (1975): "Les Chiroptères (Mammalia) du gisement pléistocène des Abimes de la Fage à Noailles (Corrèze)". *Nouvelles Archives du Musée d'Histoire Naturelle de Lyon*, 13: 57-67.

Menu, H. (1987): "Morphotypes dentaires actuels et fossiles des Chiroptères Vespertilioninés. 1^{e}. partie: étude des morphologies dentaires". *Palaeovertebrata*, 15 (2): 71-128.

– et Popelard, J.B. (1987): "Utilisation des caractères dentaires pour la détermination des Vespertilioninés de l'ouest européen". *Le Rhinolophe*, 4: 1-88.

Mitchell-Jones, A.J.; Amori, G.; Bogdanowicz, W.; Krytufek, B.; Reijnders, P.J.H.; Spitzenberger, F.; Stubbe, M.; Thisse, J.B.M.; Vorhalik, V. & Zima, J. (1999): *Atlas of European Mammals*. 484 págs. Academic Press. Londres.

Rabeder, G. (1972): "Die Insectivoren und Chiropteren aus dem Altpleistozän von Hundsheim (Niederösterreich)". *Annales des Naturhistorisches Museum, Wien*, 76: 345-474.

Schreuder, A. (1959): "La Grotte de Fontéchevade: Les Micromammifères". *Archives de l'Institut de Paléontologie Humaine de Paris*, 29: 230-240.

Sevilla, P. (1986): "Identificación de los principales quirópteros ibéricos a partir de sus dientes aislados. Valor sistemático de los caracteres morfológicos y métricos dentarios". *Doñana, Acta Vertebrata*, 13: 111-130.

– (1988): "Estudio paleontológico de los Quirópteros del Cuaternario español". *Paleontologia i Evoluciò*, 22: 113-233.

– (1990): "The fauna of bats from the upper Pleistocene locality of Santenay (Côte-d'Or, France)". *Quaternaire*, 2: 101-110

Sigé, B.; Habersetzer, J. & Storch, G. (1998): "The deciduous dentition and dental replacement in the Eocene bat Palaeochiropteryx tupaidon from Messel: The primitive condition and beginning of specialization of milk teeth among Chiroptera". *Lethaia*, 31: 349-358.

Simone, S.; Baïssas, P.; Barral, L.; Bischoff, J.L.; Bocherens, H.; Bonifay, M.F.; Bussiere, J.F.; Chaline, J.; Courant, F.; Falgueres, C.; Hennig, G.J.; Lecolle, F.; Ledru, M.P.; de Lumley, M.A., Simon, P. & Zany, D. (2002): "Assessment of the Researches about the Middle Pleistocene of Aldène Cave". *Bulletin du Musée d'Anthroplogie préhistorique de Monaco*, 42: 15-21.

Storch, G. (1974): "Quartäre Fledermausfaunen von der Insel Malta". *Senckenbergiana lethaea*, 55: 407-434.

Topál, G. (1963): "The bats of a Lower Pleistocene Site from Mt. Kövesvárad near Répáshuta, Hungary". *Annales Historico-Naturales Musei Nationalis Hungarici*, 55: 143-153.

– (1970): "*Barbastella rostrata* n. sp. from the middle Pleistocene of the Tarkö niche, North-East Hungary". *Discussiones paleontologicae*, 15: 5-18. Budapest.